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A TAXONOMIC REVISION OF *PODOCARPUS*
III. THE AMERICAN SPECIES OF *PODOCARPUS*:
SECTION *POLYPODIOPSIS*

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With one plate

Podocarpus Rospiglosii Pilger has been known only since 1923 from the type locality in Peru when Pilger (10) described an unnamed specimen in the Berlin Herbarium and noted its affinities with *P. vitiensis*, but he considered both as belonging to the section *Nageia*. This specimen was sent by Dr. C. J. Rospigliosi from the Museo de Historia Natur. de la Univers. de Lima, #556 leg. *N. Esposto*, and is represented by a photograph and fragment in the Field Museum collection of type specimens. Earlier, in 1903, Pilger (9) had recognized the similarity between *P. vitiensis*, the Fijian member of this section, and two sterile specimens from unspecified localities in the equatorial Andes (Colombia, *Stübel 171^b*, and Venezuela, *Funck et Schlimm 1208*). It was Florin (6) who revived Bertrand's (4) category *Polypodiopsis* as a section which now includes *P. vitiensis*, *P. minor* and *P. Rospiglosii*.

No specimen was available in American collections from South America until very recently when four were recognized, all in the United States National Herbarium (one of them accompanied by a seed), having been referred to *P. montanus* in section *Stachycarpus* because of the very superficial resemblance of foliage. Four recent collections from Colombia have been added by the same Herbarium and four more appeared among the plants collected in Venezuela by Steyermark of the Chicago Museum of Natural History (several with half-grown and fully mature seeds) with duplicates in the Herbarium of the University of Illinois.

Podocarpus Rospiglosii, with its flat leafy branches resembling the compound leaves of a fern, is recognizable from its external morphology. It is the only American species of *Podocarpus* with stomata on both sides of the leaf. The leaves are opposite; all other easily confused species have alternate leaves. Florin (6, 7) has shown that they are four-ranked as the

leaf traces emerge from the stele, but the leaves are twisted at the base and bent around, so that they are actually spread out in a single plane with all leaves on one side of the twig exposing their abaxial surfaces toward the observer, while the leaves on the opposite side of the twig expose their adaxial surfaces. This accounts for the differentiation in development of palisade parenchyma and stomata on the upper and lower sides of the leaf. When the abaxial surface is exposed to the light, more palisade is developed on the abaxial side and more stomata on the adaxial. When the adaxial surface is exposed to the light, little or no palisade may be developed on the abaxial side. Since both sides of the leaves have stomata and can scarcely be distinguished, this peculiar phyllotaxy may be recognized externally only from the decurrent leaf bases and the characteristic twisting of these leaves that brings the four ranks into the same plane.

The number and position of the resin canals separate *P. Rospigliosii* from all known members of *Podocarpus*. It is the only American species which normally has three resin canals under the vascular bundle. Some leaves show only one, others may have five, the additional two being located under the transfusion tissue. The lateral resin canals vary in number from two to six. When there are only two, these are rarely located at the extreme margin of the blade, but an increase to four or six shows them in the margin or at the end of the transfusion tissue. These resin canals do not arise by division of existing resin canals at the base of the leaf. The largest number are present in the middle of the blade, and they disappear toward the ends. No more than eleven resin canals have been observed in any leaf and the two sides of the leaf may vary, as two on one side and three on the other. The structure of the canal is normal—a cavity of varying size bounded by a ring of resin excreting cells. In unstained cross sections, the resin in the cavity shows a greenish color.

The position of the resin canals in the section *Polypodiopsis* has been touched on twice in the literature. Bertrand (4) described one vascular and two marginal resin canals for *P. vitiensis* from Fiji. This would be the only *Podocarpus* in the western Pacific having marginal resin canals. Unfortunately, this specimen is unavailable for re-examination and examples from six localities, found in American herbaria and identified as *P. vitiensis*, have shown only the single vascular canal and no marginal ones. Mahlert (8) noted the resin canals in a specimen in the Leipzig Herbarium labelled *Polypodiopsis*, in which he found one resin canal directly under the phloem, which becomes three, and four lateral canals, one in the center of each side and one marginal. He believes this specimen to be the same as that described by Bertrand with one median and two marginal resin canals. We are wondering if some early American collections, inadequately labelled or labels lost and having found their way into European collections, may have been referred to Bertrand's section *Polypodiopsis* by comparison with material from the South Pacific. However, Mahlert describes the original three resin canals of Bertrand as dividing to

form the additional canals he observed. In *P. Rospiglosii*, there is no such branching of resin canals. It is entirely possible that Mahlert's specimen is another species in the section *Polypodiopsis* and that it is even more closely related to *P. Rospiglosii*.

Podocarpus Rospiglosii shows some leaf characteristics in common with section *Afrocarpus*. Both are amphistomatic, have hypoderm on both sides interrupted by the rows of stomata, transfusion tissue usually extending far into the blade of the leaf and large fibres reinforcing the vascular bundle, show tapered margins in cross section, and lack accessory transfusion tissue. These similarities are worthy of note in consideration of the position of the section *Polypodiopsis* in the *Podocarpus* complex.

This species is of special interest to paleobotanists since a Tertiary fossil species in this category has been found in Chile which has been the subject of considerable study. Originally the fossils in question had been referred to *Sequoia* by Engelhardt (5). They were the basis of reports of the occurrence of this genus in the Southern Hemisphere and widely quoted. Berry, who had accepted these determinations in an early treatise (1), was the first to challenge the identifications as *Sequoias* and identified one of them as *Araucaria araucoensis* (2); later he decided that none of these fossils represent *Sequoias* and referred another to *Podocarpus* as *P. Engelhardtii* (3). Florin (4), recognizing in some of these specimens the peculiar phyllotaxy with opposite paired leaves, decurrent leaf bases and especially the cuticular structures of the leaves, placed one of these fossils in the genus *Podocarpus*, *P. araucoensis* (Berry) Florin, belonging to the section *Polypodiopsis*. Thus there are according to both Berry and Florin no fossils belonging to *Sequoia* in the Southern Hemisphere based upon the original group of fossils referred to this genus. Moreover, we know definitely that members of this section *Polypodiopsis* were present on the South American continent during the Eocene.

8. *Podocarpus Rospiglosii* Pilger in Notizbl. Bot. Gard. Berlin 8: 273, 1923, in Nat. Pflanzenfam. 13: 245. 1926; Florin in Svenska Vet.-Akad. Handl. 3(10): 192-194, 275. 1931, 19: 9-12. 1940; Macbride, Flora of Peru, 1 (Field Mus. Nat. Hist. Publ. 351, Bot. ser. 13): 85. 1936; Schnee in Bol. Soc. Venezol. Cienc. Nat. 9: 183, fig. 1. 1944.

Podocarpus montanus sensu Knuth in Fedde, Repert. Sp. Nov. Reg. Veg. Beih. 43: 95. 1928, not Lodd.

An evergreen tree 30-35 m. tall with flat frondose branches and twigs, clothed with ovate-lanceolate leaves, opposite, sessile, up to 22 mm. long and 5 mm. wide in the lower parts of twigs grading down to 11 mm. long and 2.5 mm. wide toward the tips of the twigs. Leaves amphistomatic with median vein, spread out in one plane by twisting at the base with adaxial sides exposed on one side of the twigs and with abaxial sides of leaves exposed on the opposite side, as indicated externally by decurrent leaf bases and internally by orientation of xylem and phloem in vascular bundles. Buds naked. Leaves internally with hypoderm on both sides of the leaf interrupted by the stomata even at the midrib, vascular schlerenchyma of large fibres constantly present on the upper or xylem side and of smaller fibres rarely present on the lower or phloem side (not altered

by orientation). Single median vascular bundle flattened in cross section and flanked by transfusion tissue extending laterally into the leaf tissue, but no accessory transfusion tissue nor isolated sclereids in the mesophyll. Palisade tissue developed on both sides of leaf depending upon exposure. Resin canals 3–11, the median one situated beneath the vascular bundle.

“The male cones are placed at the apex of rather short, lateral axillary shoots borne by ordinary leafy branchlets. Each fertile shoot shows two to a few pairs of reduced and scale-like leaves (decussate arrangement; no twisting of the leaf bases). It carries one male cone terminally on the axis, and adjacently to this two cones in the axils of the uppermost pair of scales, and two more cones may in addition be placed in the same way, but some distance from the shoot apex.”*

Ovulate cones placed at the apex of short axillary shoots attached to the thicker branches rather than the more slender twigs. Each fertile shoot shows two growth zones belonging to two different seasons' growth. Leaves of the older part usually smaller than vegetative leaves with twisting of leaf bases unless these leaves are reduced to scales, while the last season's growth includes two to four or more pairs of broader ovate-orbicular decussate bracts (sterile cone scales) not twisted and appearing more gray-glaucous. The single inverted ovule borne in terminal position, with a single ovate bract on the side away from the micropyle. This ovular, slightly keeled bract, 4 mm. long by 3 mm. wide, persists and while essentially free from the ovule, adheres sufficiently near its base to fall away with the seed. Both ovules and seeds have a small crest at the terminal end.

Seed obovoid, 20–30 mm. long and 12–18 mm. wide, not flattened, with micropyle below. The seed coat consists of an outer layer which becomes fleshy, a stony layer 1 mm. thick and an inner layer enclosing the endosperm. Both the stony layer and endosperm plus nucellus narrow to a conical spine or point at the micropyle, but covered by the fleshy layer of the seed so that this spinelike point is not observed unless the outer layer is removed. At the opposite end near the crest the stony layer is rounded. Hence, the crest is wholly a part of the fleshy layer, and may be broken off on mature seeds. These fruits become colored from blue-black to red, have been reported as edible (presumably as nuts) and are very attractive when ripe.

DISTRIBUTION: Mountains of western Venezuela, eastern Colombia and Central Peru at altitudes between 1700 m. and 2600 m.

SPECIMENS EXAMINED:

COLOMBIA. Dept. Antioquia: *W. A. Archer 541* (with seeds in pocket) from cultivation in Fredonia [fig. 37] (†US). Dept. Cundinamarca: San Francisco, Cordillera Oriental, *Garcia-Barriga 11038* (US, [fig. 35] †Ill, with developing seeds attached); *Garcia-Barriga 11041* (†US); *Garcia-Barriga 11586* (US); Estación San Bernardo, *Dugand & Jaramillo 3962* (US).

VENEZUELA. Tachira: between La Grita and Yetuines, *Jahn 99* (†US); above La Grita, *Steyermark 57112* (F, †Ill). Merida: no locality data, *Pittier 12756* (†US); above La Carbonera, *Steyermark 56049* (F, †Ill); Canagua, *Steyermark 56370* (F, †Ill); no locality data, *Sardi 6672* (Ven, †Ill); above Jaji, *Steyermark 55999*, with ovules, mature seeds in pocket [figs. 38, 39] (F, †Ill).

* From Florin (7), who personally examined the type specimen in the Herbarium of the Berlin Museum. Most of these details may be observed under magnification in Macbride's photograph of the type specimen (F).

PERU. Prov. Junin: Oxapampa, *Esposito 556 type*, photo and fragment (†F); †fragment of Berlin specimen sent by Dr. Florin; *Soukup 1801 topotype* (†US, [fig. 36] Ill); seedling, *Soukup 1801* (Ill).

There is considerable variability in the specimens examined with respect to the size of the leaves, their internal anatomy, and the seeds. In general, young branches of vigorously growing trees and lower branches are likely to have the longest leaves, which also vary due to position on the same twig. Old trees bearing reproductive branches usually have leaves that average much smaller. The seeds are shown in figures 38 and 39. Although this material occurs in the Andes at sites from 8° north of the Equator to 12° south latitude, the variations were found to intergrade and not to separate into categories. Only careful observations by field collectors and foresters will determine the existence of sub-species or varieties.

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EXPLANATION OF PLATE

PLATE V

FIGS. 35-39. *Podocarpus Rospiglosii* Pilg. FIG. 35. *Garcia-Barriga 11038* (Ill) showing numerous female cones with single terminal ovules enlarging after pollination. This specimen has the smaller leaves usually associated with reproductive branches $\times \frac{7}{8}$. FIG. 36. Twig from *Soukup 1801* (Ill) from vegetative branches with larger leaves. $\times \frac{7}{8}$. FIG. 37. *Archer 541* (US) Central part and one side of transverse section, above middle of leaf, showing 6 of its 9 resin canals. Vascular bundle has flattened form in cross section, but at this level, the transfusion tissue is not always developed into extreme wing-like extensions (cf. FIG. 4). Leaves are amphistomatic; hypoderm is interrupted (always where there are stomates occasionally in places without stomates) on both sides of leaf. $\times 60$. FIG. 38. Seed from *Steyermark 55999* (Ill). Bract may be seen at back of seed away from micropyle. $\times \frac{7}{8}$. FIG. 39. Old seeds collected from litter under tree of same, showing seed intact at center, with outer layer partially removed at left and right, exposing micropylar spine-like extensions below $\times \frac{7}{8}$.

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